GOOD AND BAD TRAITS OF *HARMONIA AXYRIDIS* –FROM BIOLOGICAL CONTROL TO INVASION

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ABSTRACT.

The ladybird, *Harmonia axyridis*, was introduced from Asia as a biological control agent of aphid and coccid pests and has been very successful in this respect. The coccinellid established but became invasive in surrounding regions and has been reported to have undesirable negative impacts on native aphidophagous guild members, cause nuisance problems in residential areas and also plant damage. This makes *H. axyridis* an excellent case study to identify the traits that make a predator an attractive and effective biological control agent and those that lead us to categorise it as an alien invasive species. A number of these traits can be both "good" and "bad" when viewed in either a biological control context or in an ecological context. In this paper we discuss the relative merits of traits that are commonly associated with biological control agents (voracity, prey searching efficiency, tolerance to pesticides) along with those less often considered, but that we believe are of equal importance, including overwintering potential, phenotypic adaptability and intraguild interactions with native aphidophagous species. The consequences of these traits on species diversity and the control of pest species in the introduced range will be discussed.

HARMONIA AXYRIDIS AS A BIOLOGICAL CONTROL AGENT AND ITS ESTABLISHMENT IN EUROPE.

The multicolored Asian ladybird *Harmonia axyridis* (Pallas) (Coleoptera: Coccinellidae) is indigenous to a vast region enclosing China, Japan, Korea, Mongolia and Siberia (Brown *et al*. 2008a). Because of its high voracity and good prey searching ability, ease of rearing, wide food range and ability to colonize a wide range of habitats, the species has been used in biological control strategies in America and Europe (e.g. Brown *et al.* 2008a; Coutanceau 2006; Koch 2003). *Harmonia axyridis* was initially released as an exotic classical biological control agent against non co-evolved pest species and intended to establish and maintain self perpetuating control of pest species at the release sites. Due to its highly dispersive nature *H. axyridis* did not remain at the release sites necessitating the repeated release of *H. axyridis* and the adoption, in some areas, of an augmentation biological control approach in which establishment was no longer expected or desired. Several studies have reported the species to be a successful biological control agent in

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various crops against a number of economically important aphid pests (reviewed in Hodek & Honek 1996; Koch 2003; Lucas *et al.* 2007a; Tedders & Schaefer 1994). However, in several areas where it had been augmented it established and quickly became invasive. A detailed description of the species' introduction and invasion history can be found in Koch (2003), and Koch & Galvan (2008) for North and South America and in Brown *et al.* (2008a) and Coutanceau (2006) for Europe. In some cases adverse impacts on native biodiversity, the fruit and wine industry and inhabitants of buildings in which the species overwinters en masse have been reported (Adriaens *et al.* 2008; Koch 2003). Public concern for the potential risks *H. axyridis* poses to the environment, humans and crops has raised awareness that beneficial and potentially negative properties of an exotic natural enemy need to be evaluated and acted upon before release as a biological control agent.

FUNCTIONAL TRAITS OF *H. AXYRIDIS.*

The particular biological attributes, or traits, of *H. axyridis* relate to how it functions as a predator and have evolved to ensure that it is well adapted to conditions in its native range and the ecological niche that it fills. They also determine its potential as an effective biological control agent, but also its likelihood of having negative consequences for the environment if exploited for biological control, particularly beyond its native range. Here we describe these attributes, discuss their consequences and use them to identify those that are the strongest drivers, alone or in combination, of negative consequences and are, therefore, of greatest relevance for risk assessment of biological control agents.

Foraging efficiency and prey range.

As one of the largest predatory coccinellids, *H. axyridis* consumes up to 370 aphids during larval development and up to 800 aphids in its lifetime (Koch 2003; Soares *et al.* 2001). This coupled with a well adapted search strategy makes *H. axyridis* a formidable predator (Hodek & Honek 1996; Koch 2003; Obata 1986).

Unlike many species of coccinellid, *H. axyridis* is highly polyphagous. Arthropod pest species attacked include numerous aphid species but also species in Tetranychidae, Psyllidae, Coccoidea, Chrysomelidae, Curculionidae and Lepidoptera (e.g. Hodek & Honek 1996; Koch 2003; Lucas *et al.* 2007a; Tedders & Schaefer 1994). However, polyphagy also means that *H. axyridis* has the potential to prey on non-target arthropods. Experimentation has shown that these can include species of conservation concern like the monarch butterfly (Koch *et al.* 2006) and beneficial species within the natural enemy guild such as the immature stages of predators and parasitoids as well as fungal pathogens (see Pell *et al.* 2008 and references therein).

When insect prey are scarce *H. axyridis* can exploit plant foods like pollen and nectar (Berkvens *et al.* 2008a). Pollen is a suboptimal food as larval survival and adult fecundity are both significantly reduced compared to individuals feeding on lepidopteran eggs (Berkvens *et al.* 2008a). However, it could provide a mechanism for survival in the absence of prey that most other species of coccinellid do not have (Berkvens *et al*. 2008a; Hodek & Honek 1996; unpublished data). Unlike many predatory coccinellids, *H. axyridis* can also be frugivorous in the autumn, which is believed to increase winter survival of adults (Galvan *et al.* 2008; Koch *et al.* 2004a).

Reproductive capacity.

Harmonia axyridis is multivoltine and does not require a period of diapause before reproduction. In its native and invasive range *H. axyridis* is usually bivoltine (e.g. Adriaens *et al.* 2008; Brown *et al.* 2008a; Koch 2003), but more than two generations per year can also occur, with up to four generations per year in Greece (Katsoyannos *et al.* 1997), facilitating rapid population build up. *Harmonia axyridis* females produce large numbers of offspring and can be long lived. Females can lay between 20 and 30 eggs per day, live for between 60 and 140 days with a long oviposition period, between 30 and 100 days (Agarwala *et al.* 2008; Berkvens *et al.* 2008b; Hodek & Honek 1996; Mignault *et al.* 2006; Soares *et al.* 2001), depending on the nature and abundance of prey. There are even reports of females living for 3 years and still ovipositing in their third year (Hodek & Honek 1996).

Climatic adaptability.

Development and reproduction of *H. axyridis* is optimal between 15 and 25°C but only limited below 11°C and above 35°C, and they easily tolerate subzero temperatures (Acar *et al.* 2004; LaMana & Miller 1998; Schanderl *et al.* 1985). In a number of studies in the USA and Japan, the lower lethal temperature was between -11.9°C and -19°C (Koch *et al.* 2004b; Watanabe 2002). Overwintering adult *H. axyridis* collected from Belgium, Europe had a similar degree of cold tolerance (-15 to -19°C) to those collected by Watanabe (2002) (Berkvens *et al.* unpublished data). Using the CLIMEX model Poutsma *et al.* (2008) predicted the potential geographic distribution of *H. axyridis* based on climatic variables. In addition to the countries in temperate Europe and North America in which the species has already established, the model predicted that the species could also establish in a large part of Mediterranean Europe, South America, Africa, Australia and New Zealand.

Habitat adaptability.

Harmonia axyridis is primarily categorized as an arboreal species. Favoured arboreal habitats in Belgium, for example, include lime (*Tilia* sp.), maple (*Acer* sp.), willow (*Salix* sp.), oak (*Quercus* sp.), birch (*Betula* sp.), pine (*Pinus* sp.) and hawthorn (*Crataegus* sp.), but nettle (*Urtica dioica* L.(Urticales: Urticaceae)) and reed (*Phragmites australis* Steud (Cyperales: Poaceae)) are also frequently visited (Adriaens *et al*. 2008). However, unlike many coccinellids that are habitat specialists, *H. axyridis* can be considered eurytopic as it is found in a vast range of semi-natural, agricultural and even urban habitats (e.g. Adriaens *et al.* 2008; Brown *et al.* 2008b; Lucas *et al.* 2007b).

Dispersal capacity.

Harmonia axyridis has a high dispersal capacity. In North America it spread over an area of nearly 150 000 km^2 during the two years after it initially established in 1988 in south-eastern Louisiana (Tedders & Schaeffer 1994). In Europe it has established in 13 European countries in the nine years after it was first recorded in the wild in 1999 (Brown *et al.* 2008a). High dispersal rates for individual *H. axyridis*

adults are evident in the long migratory flights to their hibernation sites (e.g. Brown *et al.* 2008a; Hodek & Honek 1996).

Polymorphism and phenotypic plasticity.

Harmonia axyridis is highly polymorphic, with more than 100 recorded melanic and non-melanic elytral patterns (Soares *et al.* 2003). Recent studies indicate there is variation among the colour morphs of *H. axyridis* for different traits (e.g. food conversion, developmental time, fecundity, body size and weight, etc.), offering particular morphs greater fitness than others in specific habitats or at specific times (Berkvens *et al.* 2008 ab; Serpa *et al.* 2003; Soares *et al.* 2001, 2005;). The most prominent colour morph varies from region to region (Hodek & Honek 1996; Koch 2003), suggesting that some phenotypes are indeed favourably selected in different ecosystems (Soares *et al.* 2008). Additionally, colouration and maculation of the species can be influenced by temperature during development (Berkvens *et al.* 2008b). Thermal melanism may speed up development and allow adults to remain active at lower temperatures, thereby increasing their foraging capacity before overwintering and their competitive advantage over other predatory species lacking this strategy (Majerus 1994).

Natural defences.

Harmonia axyridis has several natural enemies including pathogens, parasitoids, nematodes, parasitic mites and certain bird species (for a full review see Kenis *et al.* 2008; Koch 2003). However, there are only a few recorded observations of these natural enemies effectively attacking or parasitizing *H. axyridis* in its invaded range. Emergence rates of the braconid *Dinocampus coccinellae* (Schrank) (Hymenoptera: Braconidae) were near to zero when attacking field-collected *H. axyridis* adults in the USA (Hoogendoorn & Heimpel 2002) and Canada (Firlej *et al.* 2005) and varied between 0 and 10 % when parasitizing European field populations (Berkvens *et al.* unpublished). Parasitism by the tachinid fly *Strongygaster triangulifera* (Loew) (Diptera: Tachinidae) in North America varied between 4.8 and 15.4% (Katsoyannos & Aliniazee 1998). *Harmonia axyridis* is less susceptible to the nematode *Steinernema carpocapsae* (Weiser) (Rhabitida: Steinernematidae) and the fungus *Beauveria bassiana* (Balsamo) (Deuteromycotina: Hyphomycetes) than other coccinellids tested (Roy *et al.* 2008; Shapiro-Ilan & Cottrell 2005). Interestingly, *H. axyridis* has a tolerance to certain insecticides, insect transgenic crops and fungicides similar to or higher than other natural enemies of aphids (for a full review see Koch 2003).

As with other coccinellid species, when attacked, *H. axyridis* has several effective defence strategies including aposematic colouration, reflex bleeding of alkaloid laden secretions, chemical defence of eggs, thanatosis and dropping behaviour (e.g. Koch 2003; Ware *et al.* 2008). Moreover, third and fourth instars have spines that provide physical protection from intraguild and higher-order predation (Soares *et al.* 2008; Ware *et al.* 2008).

BENEFICIAL AND ADVERSE CONSEQUENCES.

When we consider the functional traits of *H. axyridis*, they describe an organism that is extremely likely to establish in an ecosystem in which it is introduced. Its polyphagy allows it to persist by exploiting alternative food resources. It is also large, voracious, multivoltine and has a high reproductive rate. As such it has potential as a classical biological control agent where establishment as well as efficacy in a target habitat is a prerequisite. For augmentation biological control establishment is not desired. However, polyphagy and high reproductive capacity facilitate ease of mass rearing and ensure a large market potential against a variety of pest species. Its ability to track pest aphid population growth and tolerance for a variety of pesticides also facilitate its use in integrated pest management programs. These aspects contributed to the perception that *H. axyridis* also had utility as a commercially viable augmentative biological control agent and was how it was ultimately used most extensively.

The very same traits that can be favourable, independently, in a biological control agent also strengthen the invasive character of a species if they occur in combination, as they do with *H. axyridis*. Alongside its other traits, *H. axyridis* is also polymorphic, dispersive, eurytopic and thus adapted to exploit a wide climatic and habitat range and well able to disperse between habitats giving it the potential to go beyond establishment in a target habitat to being an exotic invader with potential for widespread negative ecological impacts in a wide range of non-target native ecosystems. Where other biological control agents may exhibit one or two traits that make them effective in pest regulation but not a risk beyond the target habitat, *H. axyridis*, has a wide range of traits that independently may be useful in biological control, but together have significant negative consequences.

Furthermore, many traits of *H. axyridis* are exhibited to an extreme degree. For example, most indigenous coccinellids in Northwest Europe only have one generation per year (e.g. Majerus & Kerans 1989) and are less fecund than *H. axyridis* (Hodek & Honek 1996), offering *H. axyridis* a higher potential population growth than the native species (Brown *et al.* 2007a) and thus a competitive advantage.

Polyphagy in *H. axyridis* does not just extend to a number of prey species within one order but to species across many orders and even beyond arthropods to plants. Direct feeding on fruit and contamination in harvested wine grapes may make *H. axyridis* an organism of plant health concern (Galvan *et al.* 2008; Koch *et al.* 2004). A potentially stronger force structuring communities as a whole is intraguild predation which occurs when two species in the same guild also engage in a trophic interaction with each other (Polis *et al.* 1989). *Harmonia axyridis* is larger and better defended than the majority of other guild members (including predators, parasitoids and pathogens) and so the outcome is usually asymmetrical in favour of *H. axyridis* (Lucas *et al.* 2007a; Pell *et al.* 2008 and references therein). Petri dish experiments represent a ‘worst case scenario’ and the outcome may be different at more realistic scales and degrees of environmental complexity, where intraguild prey can escape or avoid contact. Natural enemies in the same guild can also facilitate each others activity. For example, *Coccinella septempunctata* L. (Coleoptera: Coccinellidae) increases transmission and dispersal of the aphid specific fungal pathogen *Pandora*

neoaphidis (Remaudière and Hennebert) Humber (Zygomycota: Entomophthorales) (Pell *et al.* 1997; Roy *et al.* 1998; 2001) and *H. axyridis* has recently been shown to increase fungal transmission to a similar extent (Wells *et al*. 2008). In general, however, *H. axyridis* has been associated with declines in population densities of some native coccinellids in its invasive range suggesting that it can have a negative impact on the diversity of other guild members (e.g. Adriaens *et al.* 2008; Michaud 2002).

Intraguild interactions do not always require the mortality of the shared prey (i.e. the target pest) and can, therefore, result in a reduction in predation pressure on the target pest population – i.e. an overall reduction in biological control (Rosenheim *et al.* 1995). In single generation experiments the addition of *H. axyridis* to an aphid enemy guild did not reduce target prey suppression even when intraguild predation occurred (Aquilino *et al.* 2005; Cardinale *et al.* 2003; Ferguson and Stiling 1996; Gardiner & Landis 2006; Snyder *et al.* 2004; Snyder & Ives 2003). However, over a larger timescale *H. axyridis* could reduce the stability of the ecosystem service of pest suppression that is provided by a diversity of natural enemies buffering for each others activity in a changing environment (Gardiner & Landis 2006; Pell *et al*. 2008; Snyder & Ives 2003)

Additionally, overwintering of *H. axyridis* adults in aggregations in buildings can cause nuisance problems for humans inhabiting or working in these buildings because its aggregations can be much larger than those of native coccinellids. There have also been reports of people developing allergic reactions to the coccinellid and even reports of *H. axyridis* biting humans (Huelsman 2002; Yarbourgh *et al.* 1999).

CONCLUSIONS.

The high pest suppression potential and polyphagy of *H. axyridis* make it an attractive candidate for augmentative biological control of a number of aphid and coccid pests. In addition, the insect's establishment potential and dispersal ability would be assets for classical biological control. However, use of the predator in augmentative or classical biological control becomes far less appropriate if the potential environmental risks are considered. The very same traits underlying its value for pest suppression, contribute to the risk of unwanted effects, including its undesired establishment in non-target habitats (following augmentative releases) coupled with direct and indirect impacts on the aphidophagous guild or other non-target species and its status as an occasional plant pest. The use of a non-indigenous species for biological pest control is especially risky if the natural enemy is a generalist (Howarth 2001 and the references therein). *Harmonia axyridis* is an excellent case study to demonstrate that, like other crop protection strategies, biological control is not risk free and that risk analysis is the proper process to weigh beneficial versus potential adverse impacts of biological control agents, particularly if these are not indigenous. A risk assessment by van Lenteren *et al*. (2008) concluded that *H. axyridis* should never have been released as a biological control agent in Europe, given that evidence indicating the potential risk was available at the time of its commercialization in 1995. Although some of the potential adverse effects, for which there have been strong indications in numerous studies, may not have been realized in the field at present, few workers will challenge the conclusions of this risk assessment. Biological control can offer a safe alternative option for pest control,

particularly if it is integrated with other control options. However, it is important that our expectations of biological control are realistic and that risk assessments take into account all the functional traits of the organism to be used and their implications for the community into which the organism is released.

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